

Responses of Ensemble Neurons to Spike-Train Signals with Independent Noises: Stochastic Resonance and Spike Variability

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Abstract

Responses have been numerically studied of an ensemble of N ($=1$, 10 , and 100) Hodgkin-Huxley (HH) neurons to coherent spike-train inputs applied with independent Poisson spike-train (ST) noise and Gaussian white noise. Three interrelated issues have been investigated: (1) the difference and the similarity between the effects of the two noises, (2) the size effect of a neuron ensemble on the signal-to-noise ratio (SNR), and (3) the compatibility of a large firing variability with fairly good information transmission. (1) The property of stochastic resonance (SR) for ST noise is shown to be rather different from that for white noise. When SNR for sub-threshold inputs obtained in our simulation is analyzed by the expression given by $SNR = 10 \log_{10} [(A/X^\alpha) \exp(-B/X)]$ where X expresses the noise intensity and A and B are constants, the index α is $\alpha = 3$ for the ST noise and $\alpha = 2$ for the white noise: the former is different from the conventional value of $\alpha = 2$ realized in many non-linear systems. ST noise works less effectively for SR than white noise. (2) The transmission fidelity evaluated by SNR is much improved by increasing N , the size of ensemble neurons. In a large-scale neuron ensemble, SNR for supra-threshold inputs is shown to be not significantly degraded by weak noises responsible to SR for sub-threshold inputs. (3) Interspike intervals (ISIs) of output spikes for sub-threshold inputs have a large variability ($c_v \lesssim 0.8$), which is comparable to the data observed in cortical neurons. Despite variable firings of individual neurons, output signals summed over an ensemble may carry information with a fairly good SNR by the aid of SR and a pooling effect.

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I. INTRODUCTION

It has been controversial how neurons communicate information by spikes [1]- [6]. Much of debates on the nature of the neural code has been mainly focused on the two issues. The first issue is whether information is encoded in the average firing rate of neurons (*rate code*) or in the precise firing times (*temporal code*). Andrian [7] first noted the relationship between neural firing rate and stimulus intensity, which forms the basis of the rate code. Actually firing activities of motor and sensory neurons are reported to vary in response to applied stimuli. In recent years, however, the alternative temporal code has been proposed in which detailed spike timings are assumed to play an important role in information transmission: information is encoded in interspike intervals (ISIs) or in relative timings between firing times of spikes [8]- [10]. Indeed, experimental evidences have accumulated in the last several years, indicating a use of the temporal coding in neural systems [11]- [15]. Human visual systems, for example, have shown to classify patterns within 250 ms despite the fact that at least ten synaptic stages are involved from retina to the temporal brain [15]. The transmission times between two successive stages of synaptic transmission are suggested to be no more than 10 ms on the average. This period is too short to allow rates to be determined accurately.

The second issue is whether information is encoded in the activity of single (or very few) neurons or that of a large number of neurons (*population* or *ensemble code*). The population rate code model assumes that information is coded in the relative firing rates of ensemble neurons, and has been adopted in the most of the theoretical analysis [16]. On the contrary, in the population temporal code model, it is assumed that relative timings between spikes in ensemble neurons may be used as an encoding mechanism for perceptual processing [17]- [19]. A number of experimental data supporting this code have been reported in recent years [20]- [21]. For example, data have demonstrated that temporally coordinated spikes can systematically signal sensory object feature, even in the absence of changes in firing rate of the spikes [22].

The strong criticism against the temporal code is that spikes are vulnerable to noise while the rate code performs robustly in the presence of noise but with limited information capacity. It is well known that although firings of single neocortical neurons *in vitro* are precise and reliable, those *in vivo* are quite unreliable [23]. This is due to noisy environment *in vivo*, which makes the reliability of neurons firings worse. In recent years, however, much studies have been made for the stochastic resonance (SR) [24] [25] in which information transmission of signals is enhanced by background noises, against our conventional wisdom. SR in a neural system has been theoretically investigated [26]- [42]. The transmission fidelity for weak external signals, which is evaluated by the signal-to-noise ratio (SNR) or the peak height of the interspike-interval (ISI) distribution, is enhanced by added noises. SR is supported in some physiological experiments for biological systems such as crayfish [43] [44], cricket [45] and rat [46] [47].

Although SR itself is a generic phenomenon, its detailed character is determined by the three important factors: (a) kinds of systems (neurons), (b) input signal and (c) noises. As for the first factor of (a) neurons, SR in single neurons has been studied by using various theoretical models such as the integrate-and-fire (IF) model [26]- [28], the FitzHough-Nagumo (FN) model [29]- [31] and the Hodgkin-Huxley (HH) model [32] [33]. SR in coupled or ensemble neurons has been also investigated by using the IF model [34]- [35], FN model [36]-

[38] and HH model [39]- [42]. The transmission fidelity has maximum when the noise magnitude or the coupling strength is changed. It has been pointed out that the transmission fidelity of ensemble neurons for sinusoidal inputs with independent white noises is improved as the size of an ensemble is increased [36].

As for the second factor of (b) input signals, most of theoretical studies have been made for analog inputs with periodic (mostly sinusoidal) or aperiodic amplitude modulation [48]. This is because these studies have been motivated by a fact that peripheral sensory neurons play a role of transducers receiving analog stimulus and emitting spikes. In central neural systems, however, cortical neurons are reported to play a role of data-processors receiving and transmitting spike trains [49]. There are only a few theoretical studies on SR for spike-train inputs [50]- [54]. The response of single IF neurons to coherent spike-train (ST) inputs is shown to be enhanced by an addition of weak ST noises characterized by the Poisson [50] [51] or gamma distribution [52]. Quite recently, the present author has studied SR of ensemble HH neurons for *transient* spike-train inputs with independent Gaussian noise by using the wavelet analysis [54].

As for the third factor of (c) noises, it has been reported that noises are ubiquitous in neural systems. The origin of these noises is not clear at the moment. We may suppose, however, several conceivable origins of noises: (i) cells in sensory neurons are exposed to noises arising from the outer world, (ii) ion channels of the membrane of neurons are known to be stochastic [55], (iii) the synaptic transmission yields noises originating from random fluctuations of the synaptic vesicle release rate [56], and (iv) synaptic inputs include leaked currents from neighboring neurons [57]. Most of existing studies on SR have simulated noises of the items (i)-(iii) by the Gaussian white noise [26]- [28] [34]- [42] [54] or Ornstein-Uhlenbeck (OU) noise [29] [32] [33] [41] [42]. ST noise is employed in Refs. [50]- [53] taking account the item (iv). In our study, we will include the ST and white noises which may be regarded, in a crude sense, as analog and digital noises, respectively, with the rather different character.

One of the controversial issues concerning cortical neurons is how the neurons may communicate information by spikes with a large variability. It has been reported that the variability of $c_v = 0.5 \sim 1.0$ is observed in spike trains of non-bursting cortical neurons in visual V1 and MT of monkey [58], which is in strong contrast with a small $c_v (= 0.05 \sim 0.1)$ in motor neurons [59]. There have been much discussions how to understand the observed large variability: a balance between excitatory and inhibitory inputs [57], the high physiological gain in the plot of input current vs. output frequency [60], correlation fluctuations in recurrent networks [61], the active dendrite conductance [62], input ISIs with the distribution of a slow-decreasing tail [63], and input ISIs with large c_v [64] [65]. We expect that although there might be several origins responsible to the observed, large variability in ISI, noises may be one of conceivable mechanisms.

The purpose of the present study is to investigate responses of ensemble neurons to *spike-train* inputs subject to ST and white noises, in order to get some insight to the following issues.

- (1) Is the effect of ST noise on responses to spike-train signals, particularly on SR, different from or same as that of white noise?
- (2) Is a population or ensemble of neurons important for the fidelity of signal transmission?
- (3) Is a large variability of spikes compatible with information transmission with a fairly good SNR?

Responses of single HH neurons to various types of spike-train inputs with deterministic, chaotic and stochastic ISIs without noises, have been investigated [64]. SR for coherent spike-train inputs has been theoretically studied with single IF neurons [50]- [53]. We should note, however, that the response to applied, external stimulus of the realistic HH model [66] is rather different even qualitatively from that of the IF neuron [64] [65]. For an excitatory dc input I , the IF neuron which is classified as the type I, evokes the self-excited oscillation showing the continuous $f_o - I$ relation with a wide range of frequency f_o . On the other hand, the HH neuron, which is classified as the type II, has the discontinuous $f_o - I$ relation at the critical current, above which it shows the oscillation with a fairly narrow range of f_o . For an inhibitory dc input current, the HH neuron can fire with the so-called rebound process while the IF neuron cannot. Since the threshold-crossing behavior of the neuron is important in determining the behavior of its SR, it is necessary to re-examine SR for the spike-train inputs with the use of the realistic HH neuron model. Furthermore, since SR of single neurons is generally different from that of ensemble neurons, it is also necessary to investigate SR not only of single HH neurons but also of ensemble HH neurons.

The present paper is organized as follows. In Sec. II, an adopted model for an ensemble of N -unit ($N = 1, 10, 100$) HH neurons is described. Simulations for responses of ensemble neurons to ST signals with added ST noise, white noise, and ST plus white noises are reported in Sec. IIIA, IIIB and IIIC, respectively, where SR and the variability of ISIs are discussed. The final Sec. IV is devoted to conclusion and discussion.

II. ENSEMBLE NEURON MODEL

We assume a network consisting of N -unit HH neurons which receive the same ST signals but independent, ST and Gaussian noises through excitatory synapses. Spikes emitted by the ensemble neurons are collected by a summing neuron. A similar model was previously adopted by several authors studying SR [36] [39] [40] [54]. Dynamics of the membrane potential V_i of the HH neuron i is described by the non-linear differential equations given by

$$\bar{C} dV_i(t)/dt = -I_i^{\text{ion}} + I_i^{\text{ps}} + I_i^{\text{n}}, \quad (\text{for } 1 \leq i \leq N) \quad (1)$$

where $\bar{C} = 1 \mu\text{F}/\text{cm}^2$ is the capacity of the membrane. The first term I_i^{ion} of Eq.(1) denotes the ion current given by

$$I_i^{\text{ion}} = g_{\text{Na}} m_i^3 h_i (V_i - V_{\text{Na}}) + g_K n_i^4 (V_i - V_K) + g_L (V_i - V_L), \quad (2)$$

where the maximum values of conductivities of Na and K channels and leakage are $g_{\text{Na}} = 120 \text{ mS}/\text{cm}^2$, $g_K = 36 \text{ mS}/\text{cm}^2$ and $g_L = 0.3 \text{ mS}/\text{cm}^2$, respectively; the respective reversal potentials are $V_{\text{Na}} = 50 \text{ mV}$, $V_K = -77 \text{ mV}$ and $V_L = -54.5 \text{ mV}$. Dynamics of the gating variables of Na and K channels, m_i , h_i and n_i , are described by the ordinary differential equations, whose details have been given elsewhere [66] [64].

The second term I_i^{ps} in Eq.(1) denotes the post-synaptic current given by

$$I_i^{\text{ps}} = \sum_m g_s (V_a - V_s) \alpha(t - t_{im}), \quad (3)$$

which is induced by an input spike with the magnitude V_a given by

$$U_i(t) = V_a \sum_m \delta(t - t_{im}), \quad (4)$$

with the alpha function $\alpha(t)$:

$$\alpha(t) = (t/\tau_s) e^{-t/\tau_s} \Theta(t). \quad (5)$$

In Eqs.(3)-(5) $t_{im} = (m - 1) T_s$ is the m -th firing time with the input-signal ISI of T_s , the Heaviside function is defined by $\Theta(t) = 1$ for $x \geq 0$ and 0 for $x < 0$, and g_s , V_s and τ_s stand for the conductance, reversal potential and time constant, respectively, of the synapse.

The third term I_i^n in Eq.(1) denotes added, independent noises which consist of two terms:

$$I_i^n(t) = \sum_m \sqrt{C} \alpha(t - t_{im}^n) + \sqrt{2D} \xi_i(t). \quad (6)$$

The first term of Eq.(6) expresses Poisson ST noise, whose magnitude, C , is hereafter expressed by $\sqrt{C} \equiv g_n(V_a - V_s)$ in terms of g_n as in Eq.(3) for a later purpose, and t_{im}^n is the m -th firing time of the ST noise of the neuron i with the average ISI of μ_n . The second term of Eq.(6) denotes Gaussian white noises with the magnitude of D given by

$$\langle \overline{\xi_j(t)} \rangle = 0, \quad (7)$$

$$\langle \overline{\xi_j(t) \xi_k(t')} \rangle = \delta_{jk} \delta(t - t'), \quad (8)$$

where the overline \overline{X} and the bracket $\langle X \rangle$ denote the temporal and spatial averages, respectively.

We should remark that our ensemble neuron model given by Eqs.(1)-(6) does not include synaptic couplings among constituent HH neurons, in contrast with the coupled ensemble models [37] [41] [42]; related discussions being given in Sec. IV.

We assume that information is carried by firing times of spikes. Dividing the time scale by the width of time bin of T_b as $t = t_\ell = (\ell - 1) T_b$ (ℓ : integer), we define input and output signals summed over ensemble neurons within the each time bin by

$$W_i(t) = \sum_m \Theta(T_b/2 - |t - t_{im}|), \quad (9)$$

$$W_o(t) = (1/N) \sum_{i=1}^N \sum_n \Theta(T_b/2 - |t - t_{oin}|). \quad (10)$$

In Eqs. (9) and (10) $\Theta(t)$ stands for the Heaviside function, t_{im} the m -th firing time of inputs, and t_{oin} the n -th firing time of outputs of the neuron i when $V_i(t)$ crosses $V_z = 0$ mV from below. The time bin is chosen as $T_b = 2.5$ ms in our simulations. The fast Fourier transformation (FT) is performed for $W_o(t)$ in order to get the SNR defined by

$$SNR = 10 \log_{10}(A_s/A_n) \quad (\text{dB}), \quad (11)$$

where A_s is the signal power spectrum at a given frequency of $1/T_s$ and A_n the background noise level.

Differential equations given by Eqs.(1)-(6) are solved by the forth-order Runge-Kutta method by the integration time step of 0.01 ms with double precision. The initial conditions for the variables are given by $V_i(t) = -65$ mV, $m_i(t) = 0.0526$, $h_i(t) = 0.600$, $n_i(t) = 0.313$ at $t = 0$, which are the rest-state solution of a single HH neuron. Hereafter time, voltage, conductance, current, and D are expressed in units of ms, mV, mS/cm^2 , $\mu\text{A}/\text{cm}^2$, and $\mu\text{A}^2/\text{cm}^4$, respectively. We have adopted parameters of $V_a = 30$, $V_c = -50$, and $\tau_s = 2$. Adopted values of g_s , g_n , D , μ_n and N will be described shortly. The simulation time for each run for a given set of parameters is $T_{sim} \sim 1500$ ms ($150000 \times N$ time steps) and initial 3000 N time steps are discarded to get asymptotic solutions. The size of sample data for FT analysis becomes $N_{FT}=512$ when the input ISI is chosen to be $T_s = 25$ ms. A single simulation with $N = 100$ requires the CPU time of about 150 minutes by DOS/V PC with 900 MHz processor. The calculated SNR is expected to be improved if the simulation time T_{sim} is increased. Unfortunately, we have not been able to adopt larger T_{sim} because of a limitation in our computer facility (related discussion will be presented in Sec. IV). We hope that our simulation reveals some of the interesting features of SR of ensemble neurons for spike-train inputs with added, multiple noises.

III. CALCULATED RESULTS

A. Spike-Train Noises

1. SNR and SR

Firstly we discuss the case in which ensemble HH neurons receive input signals with independent ST noise only. The input ISI is assumed to be $T_s = 25$ ms because spikes with this value of ISI are reported to be ubiquitous in cortical brains [49]. We study sub-threshold inputs with $g_s < g_{th}$ for which neurons cannot fire without added noises. The threshold value of g_{th} generally depends on the input ISI, T_s : for example, $g_{th}=0.088$, 0.085 and 0.095 for $T_s=20$, 25 and 30 ms, respectively [67].

Raster in Fig. 1 shows firings of $N = 100$ ensemble neurons when spike-train signals of $T_s = 25$ ms are applied to ensemble neurons with added ST noises of $g_n = 0.10$, $D = 0.0$ and $\mu_n = 25$ ms. Neurons fire when a spike-train input plus noise or noises exceed the threshold level. At a glance, firings in Fig. 1 seem random. We may realize it is not true when firings are summed over ensemble neurons as shown in Fig. 2(b) where the output signal $W_o(t)$ summed over a $N = 100$ ensemble is plotted. We note that $W_o(t)$ includes a periodic component with a period of $T_s=25$ ms as an input signal shown in Fig. 2(a). This regularity is more clearly seen in its FT power spectrum shown in Fig. 3(a), which shows clear peaks at a fundamental frequency of $1/T_s = 40$ Hz and its harmonics. Information may be transmitted with aid of SR in a $N = 100$ neuron ensemble.

When the size of ensemble neurons is small, however, the information transmission is much degraded. Figures 2(c) and 2(d) show $W_o(t)$ for $N = 10$ and $N = 1$, respectively, other parameters except N being the same as in Fig. 2(b). Figure 2(d) for $N = 1$, for example, shows that a single neuron intermittently fires, yielding 18 firings for 40 input spike inputs. The FT power spectra for $N = 10$ and $N = 1$ are expressed in Fig. 3(b) and 3(c), respectively. Figures 3(a)-3(c) show that the magnitude of a peak at the fundamental

frequency divided by that of background noises, *i.e.* SNR, increases as the size of ensemble neurons is increased. These mean that despite of ostensibly irregular firings of single neurons, output signals summed over an ensemble, $W_o(t)$, become more regular when N becomes sufficiently large.

Figure 4 shows SNR as a function of g_n calculated for $g_s = 0.06$, $D = 0$ and $\mu_n = 25$ ms with $N = 1, 10$ and 100 . Results for $N= 1$ and 10 are averages of ten runs. When the noise intensity g_n is increased from zero, neurons begin to occasionally fire by a cooperative action between input signals and added noises. As g_n becomes greater than the threshold level of $g_{th} = 0.085$, ST noise alone is sufficient to trigger firings without signal inputs. When g_n is further increased, SNR of outputs is gradually degraded. Then SNR has a maximum at $g_n \sim g_{th}$, which is the characteristics of SR. For the case of $N = 10$ and 100 , we realize SR with the maximum in SNR for a weak noise of $g_n \sim 0.07$. On the contrary, for the case of $N = 1$, the maximum in SNR is not evident although SNR is enhanced at $g_n > 0.04$.

In many non-linear systems, SNR for sinusoidal input signals is reported to obey the noise-intensity dependence given by [24] [25]

$$SNR = 10 \log_{10} [(A/X^\alpha) \exp(-B/X)], \quad (12)$$

with a maximum at $X_{max} = B/\alpha$ where $X = D$ (the intensity of the white noise), $\alpha = 2$, and A and B are constants depending on the model parameters. Substituting $X = g_n^2$ [$\propto C$ in Eq.(6)], we have tried to analyze the g_n dependence of SNR for $N = 100$ obtained in our simulation. Dashed curves in Fig.4 show the results adopting two sets of parameters in Eq.(12): $(\alpha, A, B) = (2, 1.77 \times 10^{-2}, 8.45 \times 10^{-3})$ and $(3, 2.00 \times 10^{-4}, 1.27 \times 10^{-2})$, which are chosen such as to locate the maximum of SNR at $g_n = 0.065$. The latter choice of parameters with $\alpha = 3$ yields the much better agreement with the data obtained in our simulations than the former with $\alpha = 2$, although the plateau around the maximum is not well reproduced even in the latter.

We have investigated the effect of input ISI on SR by changing T_s . Solid curves in Fig. 5 denote SNRs as a function of g_n for $T_s = 20, 25$ and 30 ms obtained in our simulation and dashed curves those analyzed by Eq.(12) with $X = g_n^2$ and sets of parameters of $(\alpha, A, B) = (3, 5.01 \times 10^{-4}, 1.27 \times 10^{-2})$ for $T_s = 20$, $(3, 2.00 \times 10^{-4}, 1.27 \times 10^{-2})$ for $T_s = 25$, and $(3, 7.94 \times 10^{-5}, 1.27 \times 10^{-2})$ for $T_s = 30$. The index $\alpha = 3$ is realized for all the T_s values investigated. The maximum SNR value is decreased as T_s is increased, although the maximum position at $g_n \sim 0.065$ in SNR is not changed.

So far our discussion is confined to the sub-threshold case. We have performed simulations also for the supra-threshold inputs, adopting g_s larger than the threshold value of g_{th} . Figure 6 shows the g_s dependence of SNR calculated for ST noise only ($g_n = 0.10$ and $D = 0$) with $\mu_n = 25$ ms, and $N = 1, 10$ and 100 . When g_s is increased across the threshold value of g_{th} , SNR is discontinuously increased. SNR for the supra-threshold inputs is better than that for sub-threshold inputs, as expected. We note, however, that ensemble neurons with large N is fairly robust against weak noises relevant to SR.

2. ISI

Next we discuss the distribution of output ISIs of *individual* neurons given by

$$T_{oin} = t_{oin+1} - t_{oin}, \quad (13)$$

where t_{oin} is the n -th firing time of outputs of the neuron i . Figures 7(a)-(d) show histograms of output ISIs for $g_s=0.02, 0.06, 0.10$ and 0.14 , respectively, when ST noise of $g_n = 0.10$ is added to ST signal (see Fig. 6). In the cases of $g_s = 0.02$, ISI histograms (ISIH) nearly obey the exponential distribution as shown by dashed curve, but it vanishes at $T_{oin} < 15$ ms because a HH neuron cannot properly respond to small-ISI inputs due to its refractory period [64]. On the contrary, in the cases of $g_s = 0.10$ and 0.14 , ISIH has larger magnitudes at $T_{oin} \sim T_s$, which may be approximately expressed by the gamma-type distribution. In the case of $g_s = 0.06$, ISIH includes not only the truncated exponential distribution but also finite contributions at multiples of T_s . This change in the distribution is more clearly seen in the g_s dependence of the average (μ_o) and RMS values (σ_o) of output ISIs, which are plotted in Fig. 8. Both μ_o and σ_o are almost constant at $g_s < 0.08$, and at $g_s \gtrsim 0.10$ they are suddenly decreased. When ISIH of output spikes for $g_s < g_{th}$ is expressed by the truncated exponential distribution given by

$$P(T) \propto \Theta(T - T_L) \exp(-sT), \quad (14)$$

$\Theta(\cdot)$ being the Heaviside function and T_L the lower bound, the average and RMS values are given by $\mu_o = (1 + sT_L)/s$ and $\sigma_o = 1/s$, which yield $\mu_o = 40$ and $\sigma = 25$ ms for $1/s = 25$ and $T_L = 15$ ms. These figures are a little different from $\mu_o \sim 50$ and $\sigma \sim 35$ ms for $g_s < 0.8$ shown in Fig. 8. The difference may be attributed to the extra contribution at $2 T_s$ obtained in our simulation, as shown in Figs. 7(a) and (b). The variability defined by $c_{vo} = \sigma_o/\mu_o$ is $0.655, 0.703, 0.307$ and 0.212 for $g_s=0.02, 0.06, 0.10$ and 0.14 , respectively. When comparing Fig. 6 and Fig. 8, we note that even if the variability of ISIs of individual neurons is considerable, output signals summed over a large-scale ensemble [$W_o(t)$ in Eq.(10)] may carry information with a fairly good SNR. For example, in the case of $g_s = 0.06$, we get SNR=17.4 dB for $c_{vo} = 0.703$. This is an advantage of a neuron ensemble.

B. White Noises

1. SNR and SR

Next we discuss SR for Gaussian white noise, which is applied to our ensemble neurons instead of ST noise. Neurons occasionally fire when signal plus noise exceed the threshold level. Firings of neurons for white noises are similar to those to the ST noises shown in Fig. 1. SNR calculated as a function of D , the intensity of the white noise, for $N = 1, 10$ and 100 is plotted in Fig. 9. When the white noise intensity is increased from zero, SNR is rapidly enhanced with a maximum at $D \sim 2$ followed by a gradual decrease, which is a typical SR. Although the calculated SNR shows the SR behavior irrespective of N , it is more evident for larger N .

The dashed curve in Fig. 9 expresses SNR calculated by Eq.(12) with a set of parameters of $(\alpha, A, B)=(2, 5890, 5)$, which are chosen such as to agree with the maximum position at $D = 2.5$ in SNR for $N = 100$ obtained by our simulation. The agreement between the result of $\alpha = 2$ and our data seems satisfactory. This value of $\alpha = 2$ agrees with the results of

SR for sinusoidal input signals in HH neurons [33] [42] as well as those realized in many non-linear systems [24] [25].

Fig. 10 shows the g_s dependence of SNR for white noises only ($D = 2$ and $g_n = 0$) with $N = 1, 10$ and 100 . SNR is gradually increased as increasing g_s . In contrast with the case for ST noise shown in Fig. 6, there is no significant changes in SNR at the threshold level shown by the vertical, dashed line. A comparison of Fig. 6 and Fig. 10 shows that g_s dependence of SNR for ST noise is different from that for white noise.

2. ISI

Figures 11(a)-(d) show histograms of output ISIs for $g_s=0.02, 0.06, 0.10$ and 0.14 , respectively, when white noise of $D = 2$ is added to ST signal (see Fig. 10). ISIHS for $g_s = 0.02$ and $g_s = 0.06$ show a typical behavior with peaks at multiples of T_s whose magnitudes decrease exponentially [29] [68]. It is noted that the distribution extends up to 200 ms. As g_s is increased across g_{th} , magnitudes of the main peak at T_s are much increased as expected. Figure 12 shows the g_s dependence of the average (μ_o) and RMS values (σ_o) of ISI and the variability (c_{vo}). As increasing g_s , both μ_o and σ_o are gradually decreased with no sudden changes at $g_s \sim g_{th}$. The variability is 0.813 and 0.710 for $g_s=0.02$ and 0.06 , respectively. As g_s becomes larger than g_{th} , ISI has a larger magnitude at $T_{oin} \sim T_s$ and then the variability is decreased: c_{vo} becomes 0.528 and 0.343 for $g_s=0.10$ and 0.14 , respectively. Comparing Fig. 12 to Fig. 8, we note that g_s dependence of μ_o , σ_o and c_{vo} for white noises is rather different from that for ST noise.

C. Spike-Train plus White Noises

Since neurons in real neural systems are in the environment with various kinds of noises as discussed in Sec. I, it is necessary to examine various effects of multiple types of noises. Taking into account independent Gaussian and OU noises, Liu, Hu and Wang have investigated the effect of spatial correlation on SR in coupled HH neurons [42]. Recently Lindner and Schimansky-Geier [35] have included, in the ensemble IF model, the additive and signal-coded noises, which are expressed by $\sqrt{2D_1} \xi_1(t)$ and $\sqrt{D_2 s(t)} \xi_2(t)$, respectively, in terms of the external sinusoidal signal $s(t)$ and Gaussian noises ξ_n with the magnitudes of D_n ($n = 1, 2$).

In previous Sec. IIIA and Sec. IIIB, we have separately discussed ST and white noises. Now we simultaneously add both the noises to our ensemble neurons. Figure 13 shows the three-dimensional plot of SNR for $N = 100$ as functions of g_n and D . In the case of $D = 0$ (ST noise only), SNR has a maximum at $g_n \sim 0.07$, as shown in Fig. 4. In the case of $g_n = 0$ (white noises only), on the other hand, SNR has a maximum at $D \sim 2$ as shown in Fig. 9. The contour plot depicted in the base of Fig. 13 shows that SNR is rapidly increased from zero as ST or white noise is increased. SNR in the presence of weak white noise of $0 < D < 1$ is enhanced by a further addition of ST noise and it depends considerably on g_n . With stronger white noise of $D > 1$, SNR is slightly enhanced by an addition of weak ST noise of $g_n \sim 0.01$ although it only weakly depends on g_n at $g_n > 0.02$. SNR in the presence of weak ST noise with $g_n < 0.05$ is much enhanced by a further addition of white noise. We

note, however, that white noise enhances SNR even in the presence of stronger ST noise of $g_n > 0.1$, where SNR is decreased by excess ST noise for $D = 0$. These clearly show that white noise is more effective for SR than ST noise.

IV. CONCLUSION AND DISCUSSION

In previous Sec. III, the simulation time of each run has been limited to be 1500 ms ($150000 \times N$ time steps) because of a limitation in our computer facility. It is, however, possible, to extend the simulation time when the simulation is made only for single ($N = 1$) neurons. Figure 14 shows SNR as a function of g_n for ST noise added to single HH neurons, which are calculated with the simulations times of $T_{sim} = 1500, 3000, 6000$ and 12 000 ms, yielding FT-data sizes (N_{FT}) of 512, 1024, 2048 and 4096, respectively. We note that as T_{sim} becomes larger, SNR is improved, in particular, its maximum becomes more evident. The dashed curve expresses SNR calculated by using Eq.(12) with $X = g_n^2$ and a set of parameters of $(\alpha, A, B) = (3, 6.31 \times 10^{-5}, 9.75 \times 10^{-3})$, which are chosen to reproduce SNR calculated for $T_{sim} = 12000$ ms with the maximum at $g_n = 0.057$. Again the index of $\alpha = 3$ is realized for ST noise added to single neurons. We note from Figs. 4 and 14 that SR becomes more significant if the duration of applied, coherent spike trains is longer and/or the size of ensemble neurons is larger. Even if the duration of applied signal is not long, SNR may be improved if the size of ensemble neurons is sufficiently large. This is more evident when the input signal is *transient* spike train, as recently demonstrated in Ref.[54].

In a summary, we have numerically investigated SR responses of an ensemble of HH neurons to spike-train signals with added ST and/or white noises. Our conclusions against the three issues raised in the Introduction are summarized as follows:

- (1) Comparisons of Figs. 4, 6, 7 and 8 for ST noise with Figs. 9, 10, 11 and 12 for white noise, respectively, clearly show both the difference and the similarity between the effects of ST and white noises. Although SR is a genetic phenomenon, its detailed behavior depends on kinds of the input signal and added noises. When analyzing SNR obtained in our simulations with the use of Eq.(12), we get $\alpha = 3$ for ST noise, which is different from $\alpha = 2$ for white noise. ST noise is less effective for SR than the white noise (Fig. 13).
- (2) SNR is more improved as the size of ensemble is larger. In a large neuron ensemble, the transmission fidelity for supra-threshold inputs is not significantly degraded by weak noises responsible to SR for sub-threshold inputs (Figs. 6 and 10).
- (3) The variability of ISIs of individual neurons for sub-threshold inputs is rather large ($c_{vo} \lesssim 0.8$). Nevertheless the output W_o summed over an ensemble may carry information with a fairly good SNR.

The item (2) is consistent with the results of SR for transient spike-train signal [54] and for analog signals [36], showing that a population of neurons plays a very important role for the transmission of spike-train inputs both with sub- and supra-threshold levels. It is worth to note that this enhancement in SNR is due to the *pooling effect* [5] because our ensemble neuron model have no couplings among HH neurons. The item (3) shows that noise may be one of conceivable mechanism yielding a large variability observed experimentally [58]. Even when the variability of firings of individual neurons is considerable, firings summed over a ensemble may carry information with a fairly good SNR enhanced by SR and pooling

effects. Thus the large variability and high SNR are not incompatible in a large-scale neuron ensemble.

The present study entirely relies on simulations. It would be interesting to theoretically elucidate the dependence of the index α on a kind of added noises mentioned above. However, conventional approaches having been employed for a study of SR such as the rate-equation and linear-response theories [24]- [25], do not work on our case. We leave its analytical study as our future problem.

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FIGURES

FIG. 1. Raster showing firings in $N = 100$ ensemble neurons with $D = 0.0$, $g_n = 0.10$, $\mu_n = 25$ ms and $g_s = 0.06$ (ST noise only).

FIG. 2. (a) An input signal $W_i(t)$, and (b) output signals $W_o(t)$ for $N = 100$, (c) $N = 10$ and (d) $N = 1$, with $D = 0.0$, $g_n = 0.10$, $\mu = 25$ ms and $g_s = 0.06$, results of (b) and (c) being multiplied by factors of 5 and 2, respectively.

FIG. 3. Fourier power spectra for (a) $N = 100$, (b) $N = 10$ and (c) $N = 1$, with $D = 0.0$, $g_n = 0.10$, $\mu_n = 25$ ms and $g_s = 0.06$.

FIG. 4. The g_n dependence of SNR for ST noise with $D = 0.0$, $\mu_n = 25$ ms and $g_s = 0.06$, results for $N = 1$ and 10 being averages of ten runs. Dashed curves express SNR calculated by Eq.(12) with $X = g_n^2$ for $\alpha = 2$ and 3 (see text).

FIG. 5. The g_n dependence of SNR for ST noise and input signals with $T_s = 20$, 25 and 30 ms ($N = 100$, $D = 0.0$, $\mu_n = 25$ ms and $g_s = 0.06$), dashed curves expressing SNR calculated by Eq.(12) with $X = g_n^2$ for $\alpha = 3$ (see text).

FIG. 6. The g_s dependence of SNR for ST noises with $D = 0.0$, $g_n = 0.10$ and $\mu_n = 25$ ms, results for $N = 1$ and 10 being averages of ten runs and the dashed line the threshold value of $g_{th} = 0.085$.

FIG. 7. Histograms of output ISIs of $N = 100$ ensemble neurons for (a) $g_s = 0.02$, (b) 0.06, (c) 0.10 and (d) 0.14, with input signals of $T_s = 25$ ms and added ST noise ($g_n = 0.10$, $D = 0$). Dashed curves in (a) and (b) express the exponential distribution given by $P(T) \propto \exp(-T/25)$ and histograms of (c) and (d) are multiplied by a factor of 1/5.

FIG. 8. The g_s dependence of the average (μ_o) and RMS values (σ_o) of ISI, and the variability (c_{vo}) when ST noise of $g_n = 0.10$ is added to $N = 100$ ensemble, the dashed line denoting the threshold value of $g_{th} = 0.085$.

FIG. 9. The D dependence of SNR for white noises with $g_n = 0.0$, $\mu_n = 25$ ms and $g_s = 0.06$, results for $N = 1$ and 10 being averages of ten runs. The dashed curve expresses SNR calculated by Eq.(12) with $X = D$ for $\alpha = 2$ (see text).

FIG. 10. The g_s dependence of SNR for white noises with $D = 2.0$, $g_n = 0.0$ and $\mu_n = 25$ ms, results for $N = 1$ and 10 being averages of ten runs and the dashed line the threshold value of $g_{th} = 0.085$.

FIG. 11. Histograms of output ISIs of $N = 100$ ensemble neurons for (a) $g_s = 0.02$, (b) 0.06, (c) 0.10 and (d) 0.14, with input signals of $T_s=25$ ms and added white noise ($D = 2$, $g_n=0$), histograms of (c) and (d) being multiplied by a factor of 1/3.

FIG. 12. The g_s dependence of the average (μ_o) and RMS values (σ_o) of ISI, and the variability (c_{vo}) when white noises of $D = 2.0$ is added to $N = 100$ ensemble, the dashed line denoting the threshold value of $g_{th} = 0.085$.

FIG. 13. The three-dimensional plot of SNR as functions of g_n and D for $\mu_n=25$ ms and $g_s = 0.06$, the contour plot being shown in the base of the figure.

FIG. 14. The g_n dependence of SNR for single ($N = 1$) HH neurons with ST noise calculated by changing T_{sim} (ms), the simulation time for each run ($D = 0$, $\mu_n = 25$ ms and $g_s = 0.06$), the result for $T_{sim} = 1500$ ms being the average of ten runs. The dashed curve denotes SNR given by Eq.(12) with $X = g_n^2$ and $\alpha = 3$ (see text).

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